# VARIATIONS IN THE $O_g$ OF PLANT TISSUES

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(WITH FOUR FIGURES)

The physical chemists have expressed widely different views regarding the nature of osmotic pressure, but while advancing different theories in explanation of the phenomenon, they agree in the quantitative expression of the so-called pressure. If the osmometer containing the solution in question be placed into the solvent, the difference of pressure on the solution and the solvent expresses numerically the osmotic pressure of the solution in the osmometer, when a condition of equilibrium exists, *i.e.*, when no solvent flows in either direction, from or to the solution through the membrane.

The definition of osmotic pressure is illustrated in figure 1. If the

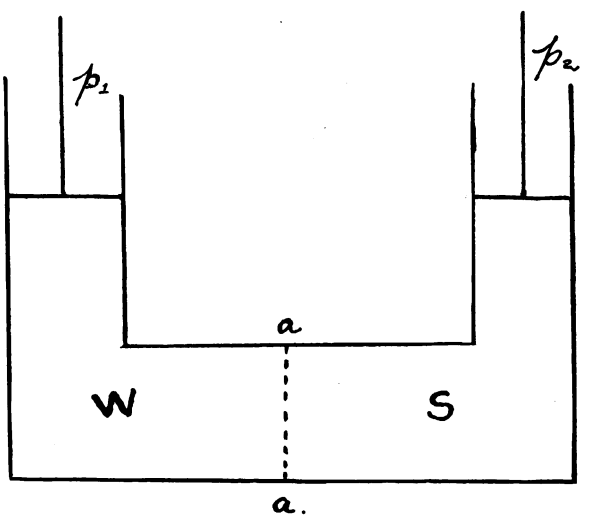


FIG. 1. A diagrammatic illustration of osmotic pressure. *W* is the solvent, *S* is the solution, *a* is the membrane; $p_2$ is the pressure on the solution, $p_1$ is the pressure on the solvent. In a condition of equilibrium $p_2$–$p_1$ is the numerical expression of the osmotic pressure.

pressure on the solution ($p_2$) is too small solvent ($W$) will flow through the membrane ($a$) into the solution ($S$). If it is too great, solvent will flow from the solution ($S$) into the solvent ($W$), passing through the membrane in the reverse direction. If the solvent fails to flow in either direction a condition of equilibrium exists at the membrane; under this condition, the difference of the mechanical pressures $p_2$ and $p_1$ expresses the osmotic pressure of the solution ($S$).

$$P = (p_2 - p_1)$$

There is nothing ideal about this quantity, it is very real; it is expressed in atmospheres.

This quantity is not under discussion in this paper and is mentioned here only to emphasize the fact, because some confusion exists about the terms in current literature on this subject.

It is practically impossible to measure the osmotic pressure of the normal cell sap directly. Some investigators measure the osmotic pressure indirectly of sap expressed from plant tissues, by the indirect cryoscopic method. This method can hardly yield results that will be helpful in determining physiological activities in plant tissues. I think this will appear from the results which are presented in this paper.

When a cell is placed into a solution of sufficient concentration, plasmolysis occurs (fig. 2). The receding film of plasm can readily be de-

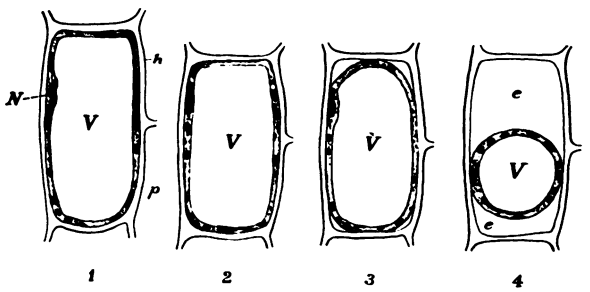


FIG. 2. Various stages of plasmolysis (After DEVRIES).

tected even at incipient plasmolysis, if the illuminating conditions are favorable. If the incipient stage of plasmolysis remains constant, the relative concentration of the plamolysing agent is taken as a measure of the relative concentration of the sap within the cell at that stage. The concentration of the agent is expressed in gram molecular units (volumetric system). This quantity which expresses the relative concentration of the cell sap at incipient plasmolysis, is termed the *osmotic value* of the cell, at incipient plasmolysis; it is symbolized by $O_g$. This quantity should always be expressed in mols and not in atmospheres. If the equivalent atmospheres are to be expressed for any reason, evidently only such an agent should be employed for which the equivalent atmospheres of osmotic pressure have been accurately determined. For various reasons given elsewhere, cane sugar was employed as the plasmolysing agent in these studies, and when it became necessary for clearness, the formula for cane sugar was appended to the symbol for the osmotic value.

No attempt is made in this paper to draw conclusions about the relative concentration of the cell sap in the normal condition of the cell. The

object is to study variations in the value of $O_g$. When there is a variation, it indicates a variation in the *quantity* or the *nature* of the solutes in the cell sap, or a variation in both the nature and the quantity of the solutes.

Some investigators tried to show that there is an $O_g$ gradient in the direction of the flow of water in the plant. URSPRUNG and BLUM showed that there is a gradient in the quantity which expresses the potential ability of the cell to absorb water (they call it suction force), and that the $O_g$ varies irregularly. Without data on the osmotic values of the cell sap and the relative volumes of the cell in the normal condition at incipient plasmolysis and when saturated, no conclusions can be drawn about the potential ability of the cell to draw water. From this it is clear that the problems taken up here are quite different from the problems which URSPRUNG and BLUM discuss under the name of Suction Force studies.

The cells of a given tissue do not as a rule have exactly the same $O_g$. When fifty per cent. of the cells of a tissue are slightly plasmolysed, the concentration of the agent is taken as the average value; it is expressed as the $O_g$ of the tissue. Numerous tests have shown that this value is reliable, *i.e.*, different tests made at short intervals under the same conditions on a given tissue, yield the same results.

Different tissues in a given plant have widely different $O_g$'s. This will be clearly shown in the data that follow. Within limits the $O_g$ of a given tissue is characteristic for that tissue. Assimilating tissues for example have higher values as a rule, than epidermal tissues. The range of variation of $O_g$ in response to given factors, is not as great in the epidermal tissues as it is in the assimilating tissues. The $O_g$ of the guard cells varies rapidly within wide limits, under the influence of certain external factors. An example by way of illustration: During the months of March and April, a considerable number of $O_g$ measurements were made for the tissues of ivy leaves all of which were taken from the same plant. The highest value recorded for the epidermis was 0.775; the lowest 0.6; the values found most frequently was 0.65. The highest value recorded for the palisade parenchyma was 1.25, the lowest 1.05, and 1.1 the most frequent value. For the guard cells the lowest was 0.6, the highest 0.825 and the most frequent 0.65.

In table I the $O_g$ is recorded for the lower epidermis, the guard cells and the spongy parenchyma of twenty different plants. The $O_g$ seems to depend upon the nature of the plant as well as upon the environment in which the plant grows. The table has been arranged in such a way as to indicate the relation of the $O_g$ to the nature of the plant. Not more than ten minutes intervened between the measurements of the $O_g$ for the different tissues of a given plant. For any given plant the epidermal tissue invariably showed a lower value than the spongy parenchyma; the guard cells had nearly the

## TABLE I

THE $O_g$ ($C_{12}H_{22}O_{11}$) OF THE TISSUES OF LEAVES

| HERBACEOUS | | | | WOODY | | | |
|---|---|---|---|---|---|---|---|
| PLANT | LOWER EPIDERMIS | GUARD CELLS | SPONGY PARENCHYMA | PLANT | LOWER EPIDERMIS | GUARD CELLS | SPONGY PARENCHYMA |
| *Solanum nigrum* | 0.425 | 0.675 | 0.575 | *Ligustrum vulgare* | 0.65 | 0.75 | 0.975 |
| *Crambe maritima* | 0.375 | 0.65 | 0.65 | *Hybiscus syriacus* | 0.6 | 0.55 | 0.8 |
| *Hesperis matronalis* | 0.55 | 0.6 | 0.725 | *Fraxinus excelsior* | 0.775 | 0.825 | 1.1 |
| *Euphorbia lathyrus* | 0.25 | 0.275 | 0.575 | *Cytisus laburnum* | 0.675 | 0.9 | 1.075 |
| *Osmunda regalis* | 0.475 | 0.425 | 0.875 | *Robinia pseudacacia* | 0.525 | 0.7 | 0.9 |
| *Polygonum orientale* | 0.375 | 0.55 | 0.675 | *Liriodendron tulipifera* | 0.6 | 0.675 | 0.825 |
| *Musa sinensis* | 0.4 | 0.35 | 0.45 | *Hedera helix* | 0.55 | 0.575 | 0.675 |
| *Datura stramonium* | 0.3 | 0.425 | 0.55 | *Crataegus oxyacantha* | 0.55 | 0.575 | 0.85 |
| *Acanthus spinosus* | 0.475 | 0.525 | 0.625 | *Castanea sativa* | 0.575 | 0.625 | 0.775 |
| *Dioscorea batatas* | 0.35 | 0.375 | 0.6 | *Populus nigra* | 0.5 | 0.575 | 0.625 |

same value as the epidermal tissue in some cases, and widely different values in other cases. For example in *Dioscorea batatas* the value was 0.35 for the epidermis, 0.375 for the guard cells and 0.6 for the spongy parenchyma; in *Solanum nigrum* the value was 0.425 for the epidermis, 0.675 for the guard cells and 0.575 for the spongy parenchyma; among the woody plants *Hedera helix* and *Cytisus laburnum* illustrate the same point. The measurements were made on different days but always in the morning between 6:30 and 8:30. During the early hours of the day the influence of the heat and light was not yet as great as it would have been later in the day. The difference of the mean values for the herbaceous plants was 0.0875 between the guard cells and the epidermis, in favor of the guard cells; it was 0.2325 between the spongy parenchyma and the epidermis, in favor of the spongy parenchyma. The difference of the mean values for the woody plants was 0.075 between the guard cells and the epidermis, in favor of the guard cells, it was 0.261 between the spongy parenchyma and the epidermis, in favor of the spongy parenchyma. It is interesting to note that while the actual values are considerably higher in the woody plants than they are in the herbaceous, the differences of the mean values are about the same in the woody and the herbaceous plants. The average value for the epidermis was 0.3975 in the herbaceous plants and 0.6 for the woody; for the guard cells it was 0.485 in the herbaceous and 0.675 in the woody; for the spongy parenchyma it was 0.63 in the herbaceous, and 0.861 in the woody plants.

The results of the experiments, which were carried out to demonstrate the variation of the guard cells in response to the natural factors which influence the plants during the day, are recorded in table II. The values recorded for the guard cells were usually not much different from the value recorded for the epidermis of the same plant, because the readings were taken at an early hour, when the factors had not effected a great variation in the relatively short time of exposure. The measurements recorded

TABLE II

VARIATIONS OF $O_g$ IN THE GUARD CELLS IN RESPONSE TO LIGHT

| PLANT | NO. | LOWER EPIDERMIS | | GUARD CELLS | | SPONGY PARENCHYMA | | SHADED |
|---|---|---|---|---|---|---|---|---|
| | | LIGHT | SHADE | LIGHT | SHADE | LIGHT | SHADE | |
| *Sedum spurium* ... | 1 | 0.275 | 0.275 | 0.500 | 0.4 | 0.450 | 0.550 | Naturally |
| *Crambe maritima* | 2 | 0.375 | 0.375 | 0.950 | 0.625 | 0.550 | 0.550 | By umbrella |
| *Crambe maritima* | 3 | 0.375 | 0.375 | 0.950 | 0.500 | 0.550 | 0.550 | By foil |
| *Nymphaea alba* ..... | 4 | 0.300 | 0.300 | 0.550 | 0.550 | 0.500 | 0.500 | Naturally |
| *Vinca major* ..... | 5 | 0.75 | 0.75 | 1.250 | 0.950 | 0.750 | 0.750 | By foil |
| *Vinca minor* ..... | 6 | 0.65 | 0.65 | 1.300 | 0.950 | 0.750 | 0.750 | By foil |

in table II were made in the evening. Some plants were exposed to the light during the day, while neighboring plants were shaded. Except in one case, the shaded plants showed considerably lower $O_g$ in the guard cells than did the plants normally exposed to the sun. It is not surprising that the one exception (*Nymphaea alba*) behaved as it did, if the guard cells are understood to be a regulating tissue: The water supply is maximum at all times so that no high degree of regulation is necessary for the rate of transpiration. Plant no. 3, *Crambe maritima* showed the greatest variation, the plant in the shade showing a value of 0.45 mol less than the plant in the light.

A great many measurements that were made on the tissues of leaves, taken from various plants at different times of the same day, tend to show that the $O_g$ of the epidermis does not vary much, if at all, during the day, no matter if the weather be fair or rainy; the guard cells vary considerably, particularly when the weather is fair; the spongy parenchyma varies more than the epidermis, though usually not as much as the guard cells.

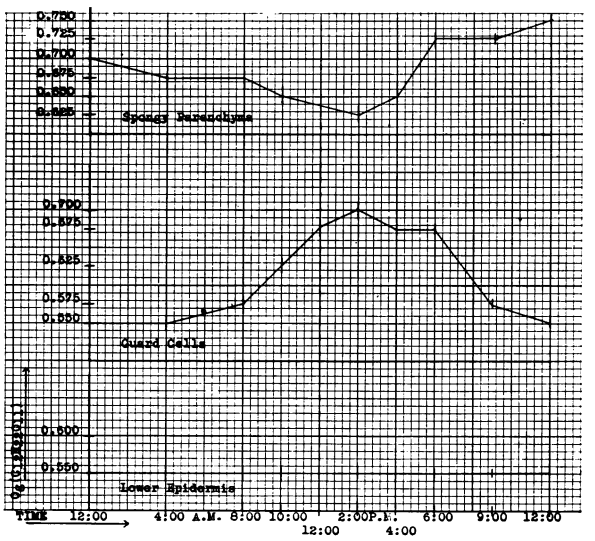


FIG. 3. Diurnal variations of $O_g$ in the tissues of an ivy leaf.

In figure 3 the graphs of the results obtained on the leaf of *Hedera helix* are given by way of illustration of the variations which occur in the epidermis, the guard cells and the spongy parenchyma, during a period of 24 hours.

The value of the epidermis remained constantly at 0.550. The guard cells had an initial value of 0.550 at midnight and at 4:00 A. M.; then an increment set in, which continued at different rates up to 2:00 P. M., at

which time the maximum value was 0.700; the greatest rate of increment was between 8:00 A. M. and noon; the rate was less from 4:00 A. M. to 8:00 A. M. than it was from noon to 2:00 P. M.; the drop from the maximum value after 2:00 P. M. was decided and sharp until 4:00, when no variation occurred until 6:00 P. M., then the decrement was sharper than after 2:00 P. M.; a slower rate of decrement set in at 9:00 and continued until midnight when the initial value of 0.550 was reached.

The variations of the spongy parenchyma were quite different from those of the guard cells. The sense of the variation was usually opposite, and the rates were different. The initial value at midnight was 0.70; there was a decrement up to 4:00 A. M. and then the value remained constant up to 8:00 A. M. (at 0.675). From that time up to 2:00 P. M. there was a decrement with a greater rate of change from 8:00 A. M. to 10:00 A. M. than from 10:00 A. M. to 2:00 P. M. The lowest value at 2:00 o'clock was 0.625. From that time a considerable increment occurred until 6:00 P. M., when the value 0.725 was reached. The value remained the same until 9:00 P. M., when a further increment was experienced up to midnight; then the maximum was reached at 0.750, which was 0.05 mol higher than the initial value.

The facts that it had rained shortly before this experiment was begun, and that during the time of the experiment the barometer was high with sunshine during the day, might be helpful in interpreting these interesting results.

Other plants were examined and found to respond in the same sense, but not always in the same degree. Among these I wish to mention, *Vinca minor, Vinca major, Cydonia japonica, Evonymus japonica, Acer negundo, Musa sinensis, Canna, Datura stramonium, Nasturtium officinalis, Solidago canadensis, Taraxacum officinale, Plantago major, Paeonia officinalis, Caltha palustris, Sedum telephium, Sedum spurium, Sempervivum tectorum, Crambe maritima, Euphorbia lathyrus, Sinapis alba,* and *Cobaea scandens.*

As might be expected, the degree of variation was not the same in all of these plants. In *Taraxacum* for instance, the epidermis showed a slight decrement from 7:00 A. M. to 3:00 P. M. (from 0.55 to 0.525). The guard cells manifested a greater increment in *Taraxacum* than in the case of the ivy leaf just cited. At 7:00 A. M. the value was 0.55 and at 3:00 P. M. it was 0.775. The spongy parenchyma decreased its $O_g$ from 0.8 at 7:00 A. M. to 0.7 at 3:00 P. M. In *Plantago major* the maximum for the guard cells was 1.05 at 2:30 P. M. and the minimum 0.75 at 6:00 A. M. Simultaneously the spongy parenchyma showed a maximum of 0.9 when the guard cells were at minimum, and a minimum of 0.8 when the guard cells were at maximum. *Saponaria ocimoides* failed to show a variation in the spongy parenchyma, as well as in the epidermis, even though the

weather was sunny. The guard cells varied as usual but the increment was 0.1, from 0.65 to 0.75.

Time does not permit further discussion of this interesting subject. I feel convinced that the facts adduced indicate that interesting variations of $O_g$ occur in the plant under the influence of the factors of the natural environment, and that they deserve investigation along the lines suggested.

Annual variations as well as daily variations occur. The results obtained tend to show that some factors which failed to affect a tissue in a short time will eventually affect it after a longer time of exposure. This is particularly true for the epidermis. In figure 4 the graphs of results obtained on an ivy leaf are given.

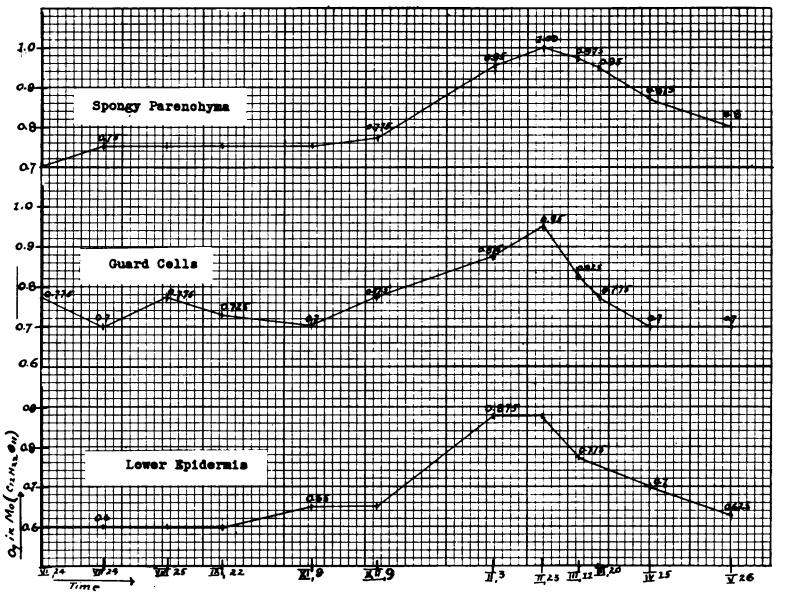


FIG. 4. Annual variation of $O_g$ in an ivy leaf.

On June 24th the $O_g$ of the epidermis was 0.6 mol, and on February 3rd of the following year it was 0.875 mol. The measurements recorded in the graph were made on the same plant which stood in garden soil, exposed to the weather for many years. All of the measurements were made at about 2:00 P. M. The guard cells were the least regular. This might be expected since they respond quickly to certain factors that might have influenced them for a short time, previous to the measurement. The variations in the spongy parenchyma are about as regular as those of the epidermis. It is particularly interesting that all of the tissues showed maximum values on February 23rd. The epidermis reached the maximum

of 0.875 mol on February 3rd already. The other two tissues continued to increase in $O_g$. The guard cells reached maximum value at 0.95, and the spongy parenchyma at 1.00 mol. The difference between maxima and minima were 0.275 for the epidermis 0.25 for the guard cells, and 0.3 for the spongy parenchyma. It is interesting that these differences are almost the same.

An explanation of these phenomena cannot be offered at present, and the facts are merely recorded for the consideration of other investigators. At some later time when the study of the different influences of certain factors on the $O_g$ of plant tissues has been completed, it is hoped that an adequate explanation may be offered. It would be very helpful in this work to know more of the effect which these factors have on the nature and quantity of the solutes of the sap.

## Summary

The $O_g$ ($C_{12}H_{22}O_{11}$) is the osmotic value at incipient plasmolysis, when cane sugar is employed as the plasmolysing agent. It is expressed in molal concentration units. This quantity must not be confounded with the osmotic pressure, nor with the concentration of the cell sap.

Variations in the $O_g$ for a given tissue can serve as an indicator of physiological activities in that tissue. Variations were studied in the epidermis, the guard cells, and the spongy parenchyma.

The $O_g$ is characteristic for a tissue. It is greater in woody plants than in herbaceous plants.

The guard cells respond quickly and considerably to the influence of certain factors in the natural environment. The response in the spongy parenchyma was evident but usually not as rapid as in the guard cells. The response in the epidermis was usually negligible or slow.

The diurnal variation was negligible in the epidermis, considerable in the other two tissues. The character of the variation was different in the spongy parenchyma and the guard cells; at times the increments were opposed in direction.

The annual variations were evident in all three tissues, the $O_g$ increased in all of them from the latter part of Spring to the end of February, when a rapid decrement set in, which continued up to Spring. The increment was least regular in the guard cells. The rate of increment was greatest in all of the tissues during the months of December and January.

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